ON THE ANATOMY OF ADEORBIS SUBCARINATUS, MONTAGU.

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PLATE VIII.

THE investigation of the anatomy of this minute Gastropod was undertaken at the suggestion of my friend Mr. E. R. Sykes, who drew my attention to the uncertainty prevailing as to the true systematic position of this molluse, and kindly offered to obtain for me some living examples from Guernsey, his great experience in shore-collecting in that island enabling him to procure living specimens almost with certainty. Mr. Sykes also provided me with references to the principal works dealing with the anatomy and affinities of this form, and he has further kindly drawn up the following short account of its habitat.

Live examples of Adeorbis are only to be found under stones of large size, that are deeply embedded in the sandy mud close to lowwater mark. The most likely stones are so large and firmly planted that one person unaided can barely lift them. The sand or mud beneath must not be too feetid. Generally it is stained yellow, and so too is that portion of the stone on which the Adeorbis is found; in fact, it is quite useless to look for live Adeorbis if the sandy mud under the stone be altogether black, as it so frequently is. The shells themselves are frequently stained yellow in places, and sometimes are partly blackened.

With Adeorbis occurs a very interesting fauna, consisting of Lepidopleurus scabridus, Jeff., Rissoia cancellata, Da C., R. lactea, Mich., R. striatula, Mont., and, occasionally, other species of Rissoia.

Adeorbis is found in Jersey, Guernsey, and Herm.

Unfortunately the weather of last summer was not propitious for shore collecting, and Mr. Sykes was only able to secure three living specimens, which he handed over to me. My own attempts to obtain Adeorbis in Sark were unsuccessful, the prevalence of strong westerly winds making collecting at low-water mark almost impracticable.

The three specimens which Mr. Sykes obtained, I was able to keep alive for some days, during which time I made a careful study of the external form of this little animal; they were afterwards preserved in alcohol, and two of them, after their shells had been decalcified, were stained, embedded, and cut into serial sections with a microtome; while from the third the radula was extracted. The small size of these animals rendered dissection almost an impossibility, so that it was deemed advisable to cut them into serial sections, in spite of the labour required in the reconstruction of the anatomy from the same.

Adeorbis is very easily kept alive for some days in a glass tube, provided that the water is changed every day or two. Here the animal shows great activity, creeping about rapidly, and moving its snout from side to side in its search for food. Duprey [1] speaks of it swimming at the surface of the water, by which I presume he means creeping, as a pond snail does by breaking through the surface film, but this habit I never observed in *Adeorbis*.

The animal is represented in the extended condition in Fig. 1 (Pl. VIII), which drawing is constructed from my studies of the

live animal.

Living specimens of *Adeorbis* were examined by Deshayes [2], who, however, gives no description of it. A live specimen was also studied by Marshall [3], who, according to Jeffreys, described it as "so red that it seemed to stain his fingers." None of my specimens,

however, exuded any such colouring matter.

The two best accounts of the external form of *Adeorbis* are those of Duprey [1] in 1876 and Fischer [4] in 1885, and of these the former is by far the most complete. Since, however, my observations differ somewhat from those of both these investigators, I have thought it advisable to give a short description of the external characters as

noted in my three living and active specimens.

External Characters of the Living Animal.—The foot, which is of a pale transparent flesh colour, is expanded and slightly notched in front, each of the antero-lateral angles being produced out into a lobe, recalling the condition seen in Valvata (Bernard [5]). These lobes, however, disappear when the foot is fully expanded, in which condition it is of oblong form, slightly narrowing posteriorly and ending in a bluntly rounded extremity; in front it exhibits that curious double margin (possibly the last trace of the propodium) so common among the Prosobranchiata. A pedal gland opens ventrally near the front of the foot. The operculum (Pl. VIII, Fig. 2) is thin, transparent, paucispiral, and littorinoid (see Jeffreys [6]), and borne on the posterior part of the foot (which does not exhibit an opercular lobe or tentacle such as seen in Rissoia), behind which it projects on the right side in Fig. 1, though when the animal is fully expanded the foot extends some distance behind the operculum.

The snout or proboscis is fairly long, club-shaped, and nonintrovertible. Through its transparent walls the brick-red, muscular buccal mass can be seen. It is flexed downwards somewhat, much as in Vivipara, and the slit-like terminal mouth is consequently ventral in position. On either side of the snout is situated a very long, thin, and slightly club-shaped tentacle; these are attached to the head above the snout. Mr. Sykes, in a drawing which he made from the living animal, has indicated a series of hair-like processes covering the swollen end of the tentacle; these I was unable to observe in any of my specimens, but their occurrence even in a single specimen is of interest, because in Rissoia parva the tentacles are conspicuously clothed with such processes. The eyes, according to Fischer and Duprey, are very small, and situated at the outer base and somewhat behind the tentacles. Examination of the living animal led me to the belief that the eyes were wanting, but subsequently, on teasing out a specimen in glycerine and examining it under

the microscope, a most minute pigment spot was discovered on each

tentacle in the position indicated above.

Projecting from the mantle cavity on the right side of the body, and even curving round the margin of the shell when the animal is fully extended and actively moving, is a large pectinate gill. This somewhat exceptional character was noted by Duprey, but Fischer neither figures nor describes it, his specimen being evidently in a moribund condition. The relations of the gill at first sight recall that of *Valvata*, but in this latter genus the gill does not extend posteriorly into the mantle cavity for any distance, whereas in *Adeorbis* the gill is well developed posteriorly on the dorsal wall of the mantle.

Two small tentacles are to be observed on the right side behind the gill (Pl. VIII, Fig. 1). These tentacular appendages of the mantle are in the position of a posterior siphon; they are not, however, grooved prolongations of the mantle margin, but solid, tentacular outgrowths. Both Fischer and Duprey appear to have overlooked these appendages, which strongly recall the single, similarly placed, tentacular thread of Valvata (Bernard [5]). Some species of Rissoia also possess such a structure which may be present on both sides of the body. Right and left tentacles in this same position also occur in Oliva and in the embryo of Vivipara. None of these forms, however, show two tentacles situated close side by side.

Internal Anatomy: The Alimentary Canal.—The mouth is armed laterally with a pair of little plate-like horny jaws, composed as in many Tænioglossa of minute chitinous tesseræ. The buccal mass is fairly large and muscular, and possesses a well-developed radula-sac.

The radula has been described and figured by Fischer [4], but as neither his figure nor his description is quite accurate, I have thought it advisable to refigure the same. The most striking feature (Pl. VIII, Fig. 3) is the lobate posterior border of the base of the central tooth. An examination of a very large series of radulæ, such as we find figured in Troschel's "Das Gebiss der Schnecken" [7], would suggest that this is a very uncommon character, only to be met with elsewhere among the Rissoiidæ; and it is with Rissoia that Fischer compares the radula of Adeorbis. When comparing the central tooth of Adeorbis with that of Rissoia, if we were to restrict ourselves to Troschel's figure of the latter, we should be compelled to admit that Fischer's eomparison was a very just one; but happening to procure a number of live specimens of Rissoia parva, for the purpose of instituting a comparison of the soft parts with those of Adeorbis, I made a preparation of the radula, and found that Troschel's figure of the central tooth was not quite accurate. The posterior border of the base of the central tooth in this form (Pl. VIII, Fig. 4) is not cleft, but entire, save for two slight indentations. It is, however, at once obvious where Trosehel made his mistake: there are on the base of this tooth two pairs of small, upstanding, backwardly directed denticles, a larger inner and a smaller outer pair, very similar to those seen in Bythinia and Paludestrina; these Troschel seems to have mistaken for the posterior border of the tooth, which latter

structure he completely overlooked, whence his representation of the

posterior border of this tooth as divided into five processes.

The most striking point of comparison between the radula of Rissoia and that of Adeorbis thus becomes one of dissimilarity, so that Adeorbis appears to stand alone in possessing the cleft base to the central tooth. Nevertheless, when we compare the whole radula of these two forms, we find that the general facies of the two are distinctly similar; this is especially noticeable in the character of the admedians and the laterals in the two forms (see Pl. VIII, Figs. 3 and 4). admedians have in both genera somewhat long bases, and well-marked denticulate free margins, provided with one large cusp, on either side of which are a number of smaller ones. The laterals when turned outwards are seen to be flattened with a distal expansion terminating in a denticulate margin. On the whole, setting on one side the basal denticle of the central tooth in Rissoia and the lobed character of the base of the same tooth in Adeorbis, I find that the radula of the latter more nearly approximates to that of the former than it does to that of any other Tenioglossate genus with which I am familiar.

A short, narrow esophagus (Pl. VIII, Fig. 5, es.) leads from the buccal mass, but soon enlarges into a complicated glaudular body (o.g.), where the lumen of the esophagus becomes split up by a series of infoldings of the wall into what appear in section to be several distinct tubes uniting both anteriorly and posteriorly; the whole forms a glandular tubular organ and appears to be comparable to the "Vorderdarmdrüse" which Haller [8] has described in Natica lineata and in Sigaretus. A pair of small salivary tubes (s.g.) are situated just in front of this organ. From the latter a long tube (cs.) runs back to the stomach (st.), which is of considerable size and divided by two constrictions into three chambers; into the posterior of these open the esophagus and the bile duct (b.d.). The intestine (int.) arises from the middle chamber, while the anterior chamber is a blind diverticulum (cr.s.), having all the relations of a crystalline style sac, and not unlike that described by Moore [9] in Typhobia and other forms. The intestine forms one or two loops in the substance of the liver, and finally crosses over to the right side opening near the anterior margin of the mantle.

Genital Organs.—Of the two specimens examined, one was a male and the other a female. The male possesses no penis, nor any accessory glands. The testis occupies the dorsal border of the visceral mass; it is a tubular gland communicating with the mantle cavity by a vas deferens, which opens high up and close to the external

orifice of the kidney.

The female genital organs consist of an ovary, containing large ova, situated behind and above the stomach; a short, narrow duct originates from this and soon passes into a large glandular tube, which after running parallel to the rectum for a short distance opens into the mantle cavity.

The excretory organ is of fair size, and opens directly into the mantle cavity near its posterior limit, without the intervention of

a long ureter.

The heart and pericardium call for no comment.

The *gill*, as already mentioned, is very large, for not merely does it occupy the usual position on the dorsal wall of the mantle cavity, but it also, when the animal is fully extended, projects beyond the

mantle (Pl. VIII, Fig. 1) as a prominent pectinate appendage.

The Nervous System.—The nerve ganglia are well developed, and closely massed round the esophagus (Pl. VIII, Figs. 6 and 7), above which latter we find a pair of large, fairly closely approximated, cerebral ganglia (c.g.), giving off nerves to the tentacles, and supplying a pair of small buccal ganglia (b.g.) in front; ventrally they give origin to a pair of delicate cerebro-pedal commissures, which join with the great pedal ganglia. These last are situated very close together, and each is divided into two (pd.g.), there being in Adeorbis a small antero-ventral lobe from which the anterior pedal nerves originate. This condition is highly suggestive of that seen in many Naticoids (Haller [8], i.e. in N. lineata and in Sigaretus). pleural ganglia (pl.g.) are situated very close behind and below the cerebral ganglia, with which they are practically fused; each gives off in front a pleuro-pedal commissure. From the left pleural a short nerve is given off; this dips down under the œsophagus, and almost immediately enlarges into the sub-intestinal ganglion (sb.g.), which extends back for a short distance under the esophagus, but the main mass of this ganglion remains on the left side of the middle line; from it a small commissure passes under the esophagus round its right side to join the right pleural ganglion.

The supra-intestinal ganglion is also situated to the left of the middle line; it is innervated from the right pleural by a nerve which crosses over the œsophagus, but it is also connected with the left pleural by a still shorter nerve. Thus we see that the zygoneurous condition is attained on both sides. But this zygoneury is a peculiar one, on account of the shortness of the commissures, and is highly suggestive of the condition seen in Lamellaria (Bouvier [10], pl. ix, fig. 40), differing from that form mainly in the closer approximation of the sub-intestinal ganglion to the left pleural; in this latter respect Adeorbis closely resembles Sigaretus, which is also doubly zygoneurous (Haller [8], pl. xiii, fig. 1), only in the latter the commissures connecting the supra-intestinal ganglion with the two pleurals are very long. A comparison with the nervous system of Rissoia (Pl. VIII, Figs. 8 and 9) shows a somewhat similar condition, for here also there is a double zygoneury, but the sub-intestinal is close to the

right pleural.

The condition of the visceral loop attained in Adeorbis, Rissoia, and Lamellaria suggests the culmination of the processes which have been apparently going on within the Naticoid series; we see there a tendency to a shortening of the commissures connecting the sub-intestinal with the right and left pleural ganglia, that on the left side being shortest in Sigaretus, while in Crucibulum that on the right is most contracted. All this tends to cause a great concentration of the ganglia around the esophagus, a condition attaining its

maximum in Adeorbis, Rissoia, Lamellaria, and Crucibulum (the latter has, however, lost its left zygoneury). Slight differences are found in the three first-named genera in the position of the supraand sub-intestinal ganglia in relation to the right and left sides of the body, this depending on the relative degree of contraction of the commissures connecting them with the pleural ganglia, but otherwise these three genera closely resemble one another in their nervous system.

A pair of well-developed otocysts are present, each situated at the postero-dorsal corner of one of the pedal ganglia, and each containing

one otolith. I was unable to trace their innervation.

The eyes, as stated above, are extremely small, and an examination of sections shows that they are vestigial structures, being reduced to a minute mass of pigment devoid of all nervous and dioptric structures.

Affinities. — Adeorbis subcarinatus was originally described by Montagu under the name Helix subcarinata, the genus Adeorbis being founded in 1842 by Searles V. Wood, who placed it between the genera Margarita and Natica; Philippi in 1844 placed it in the Paludinacea, between Fossarus and Skenea. The most striking change, however, was introduced by Gray, who in 1847 placed this Gastropod with the Trochidæ. Gray's view was adopted by Adams, Chenu, Zittel, and S. P. Woodward; the last-named, however, placed Adeorbis nearer the Turbindæ. Deshayes [2] in 1861 was the first observer to examine the living animal, and he states that it is certainly neither a Trochus nor a Turbo, but that it is either allied to the Rissoiidæ or constitutes a distinct type from all known forms. Gwyn Jeffreys, who was the first to examine the operculum, placed Adeorbis with the Solariidæ, a view which was accepted by Tryon (Man. Conch) in 1883.

It was not, however, till 1885, when Fischer [4] examined the radula, that Adeorbis was definitely proved to belong to the Tænioglossa, and he concludes that it has affinities with Rissoia, while in its conchological characters it approaches Skenea. In view of Fischer's work it is difficult to understand why Bucquoy, Dautzenberg, and Dollfus [11] still place the family Adeorbidae between the Turbinidæ and the Haliotidæ, especially when they themselves state that Fischer has definitely shown Adeorbis to be Tænioglossate.

It will be seen from the above that there has been a considerable difference of opinion in the past regarding the systematic position of *Adeorbis*, the most generally accepted view being that it finds its

nearest allies in the Rissoiidæ.

A comparison of the animal and its organs with other Prosobranchs brings us to the following conclusions:—Adeorbis is a typical Tænioglossate, as shown by its radula, which most nearly resembles that of Rissoia, while differing therefrom in the character of the median tooth, and which is totally unlike the Naticoid radula. The operculum is Littorinoid as in Rissoia, some Naticoids, and so many other Tænioglossa, but it is unlike that of Skenea; the characters of the foot, gill, and tentacular appendage suggest the similar organs

in Valvata; the esophageal glandular swelling is distinctly Naticoid; the nervous system very closely approaches that of Lamellaria,

Sigaretus, and Rissoia.

Thus we find that Adeorbis combines the characters of the Rissoiidæ and certain of the Naticidæ, but still it differs in several important respects from either of these families; consequently I should be inclined to retain the family Adeorbidæ and place the same in a position between the two families mentioned, regarding it on account of its radula as somewhat more nearly allied to the Rissoiidæ.

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EXPLANATION OF PLATE VIII.

Adeorbis subcarinatus, as seen creeping on the side of an aquarium: not fully extended.

Operculum of Adeorbis. 3. Radula of Adeorbis. ,,

4. Radula of Rissoia parva. ,,

5. Alimentary canal of Adeorbis (diagrammatic).

6. Restoration of the nervous system of Adeorbis, from above.

7. Ditto, side view.

8. Ditto of Rissoia, from above.

9. Ditto, side view.

b.d. bile duct. b.g. buccal ganglion. b.m. buccal mass.

e.g. cerebral ganglion.

cr.s. crystalline style sac. int. intestine.

otocyst. n. œsophagus. $\alpha s.$

o.g. esophageal glandular swelling.

pd.g.pedal ganglion. pleural ganglion. pl.g.

rectum. r. r.s. radula sac.

sb.g.sub-intestinal ganglion. s.g.salivary glands.

supra-intestinal ganglion. sp.g.

stomach.